

Emotional expectations influence neural sensitivity to fearful faces in humans: An event-related potential study

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The present study tested whether neural sensitivity to salient emotional facial expressions was influenced by emotional expectations induced by a cue that validly predicted the expression of a subsequently presented target face. Event-related potentials (ERPs) elicited by fearful and neutral faces were recorded while participants performed a gender discrimination task under cued ('expected') and uncued ('unexpected') conditions. The behavioral results revealed that accuracy was lower for fearful compared with neutral faces in the unexpected condition, while accuracy was similar for fearful and neutral faces in the expected condition. ERP data revealed increased amplitudes in the P2 component and 200–250 ms interval for unexpected fearful versus neutral faces. By contrast, ERP responses were similar for fearful and neutral faces in the expected condition. These findings indicate that human neural sensitivity to fearful faces is modulated by emotional expectations. Although the neural system is sensitive to unpredictable emotionally salient stimuli, sensitivity to salient stimuli is reduced when these stimuli are predictable.

negative bias, facial emotions, emotional expectation, event-related potential

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Adaptive behavior requires the fast detection of salient events, and the generation of rapid responses to these events in changing environments [1,2]. In real-life situations, salient events are often emotionally relevant, and the occurrence of emotional events is unpredictable in many cases [3,4]. In addition, the valence of an emotional stimulus (i.e., whether it is positive or negative) is often processed in the absence of prior expectations [3,5–10]. A number of studies using images from the international affective picture system (IAPS) or emotional facial expressions have consistently reported that unpredictable salient stimuli are preferentially processed over predictable stimuli [3,11], possibly due to an evolutionary benefit of heightened sensitivity to unexpected

danger. In addition, some recent ERP studies have demonstrated that the human brain is particularly sensitive to the valence strength of negative stimuli, with greater neural reactions to intense versus mild negative stimuli when the occurrence of these stimuli is unpredictable [3,4,10].

However, emotional events in real life settings are not always unpredictable [12–16]. In social interactions, individuals often anticipate others' emotional reactions using a range of cues including voices, postures, and faces [17,18]. Unpredictable emotional events are likely to be more biologically important than predictable events, since cognitive resources devoted to processing such events cannot be mobilized beforehand. Consequently, unpredictable events would be expected to elicit greater neural responses than predictable events [15]. For example, detecting a snake creeping through the grass would be expected to trigger a

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more intense emotional response than watching a signposted snake exhibition in the zoo. In the former example, the emotional event is unpredictable, and corresponding intense emotional reactions would be expected. By contrast, the processing of emotional events in the latter situation would benefit from cue-based expectations, resulting in prior mobilization of coping strategies, which would be expected to reduce the consequent emotional reaction. Using magnetoencephalography (MEG), Onoda *et al.* [15] observed that visually evoked magnetic brain responses to emotionally salient scenes were modulated by anticipation, with predictable negative images eliciting smaller visual evoked field responses compared with unpredictable images.

In real-life settings, facial expressions constitute a class of salient stimuli that convey important nonverbal information to other species members. In humans, these expressions are immediate indicators of affective disposition [1,19,20]. For instance, one may anticipate whether a person is likely to be aggressive based on their facial expression. Fearful facial expressions, which may indicate the presence of danger in the surrounding environment, would be expected to be of particular biological importance because the fast detection of fearful expressions in species members can be beneficial to survival [21,22]. Consequently, the brain appears to be particularly sensitive to fearful facial expressions [23,24]. In accord with this notion, a number of ERP studies have consistently revealed that fearful expressions elicit P1 and face-sensitive N170 components of a greater amplitude than positive or neutral facial expressions, regardless of the specific experimental paradigm used [25–30].

Although ERP techniques have a high temporal resolution, to date no studies have used ERPs to examine the effect of expectation on neural sensitivity to fearful facial expressions, and the temporal features of the underlying electrophysiological activity. Based on the evidence discussed above [15,23], we hypothesized that neural sensitivity to fearful facial expressions might vary as a function of emotional expectation. Specifically, in accord with prior studies in which emotional stimulus presentation was unpredictable, we predicted that unpredictable fearful faces would evoke enhanced reactions in specific ERP components compared with unpredictable neutral faces [6,7,31–33]. By contrast, we predicted that heightened emotional responses to fearful faces would be reduced, or even absent, when the emotional content was predictable. This effect would be manifested by similar ERPs being elicited by fearful and neutral faces in the expected condition.

The present study employed a modified cueing paradigm in which the valence of a cue image validly indicated the emotional expression of the subsequent face. Therefore, in the ‘expected’ condition, participants would be expected to form a clear expectation about the emotional content of an upcoming face upon the presentation of a cue image

[14,15,34–37]. By contrast, in the ‘unexpected’ condition, emotional faces were preceded by a fixation cross instead of a cue picture. To avoid task-relevant effects that may have obscured the electrophysiological effects of emotion processing [7], this study used an implicit emotional task that did not require participants to evaluate the emotional expressions of the target faces. Instead, participants were instructed to discriminate the gender of faces, irrespective of their emotional salience, to allow emotional responses in the laboratory to more closely resemble those in natural settings [3,18,38].

1 Materials and methods

1.1 Participants

14 undergraduate students (seven males) with a mean age of 20 years participated in the experiment as paid volunteers. All participants were healthy, right handed, reported normal or corrected to normal vision, and had no history of affective disorders. All participants gave written informed consent before taking part in the experiment. The experimental procedure was in accord with the ethical principles of the 1964 Declaration of Helsinki [39].

1.2 Materials

Face stimuli consisted of 16 face photographs (four females and four males displaying fearful or neutral expressions) taken from the Facial Expression of Emotion: Stimuli and Tests (FEEST) set [40]. Each photograph depicted a single face, with the hair and other non-facial features removed. In total, 32 emotional pictures (16 fearful pictures, 16 neutral pictures) were selected from the Chinese Affective Picture System (CAPS) to serve as pre-face cues, the valence of which validly predicted the emotional content of the subsequently presented facial expression [41].

The fearful cue pictures used in the experiment were taken from a set of 135 pictures and were validated by another group of participants ($N=49$). These participants were recruited to rate the degree of fear shown by each face using a 3-point scale (1=neutral, 3=highly fearful). The 16 fearful faces were consistently rated by all participants as highly fearful (i.e., scored as a “3”). The paired neutral cue pictures were selected in such a way that the fearful and neutral picture sets differed significantly in valence (mean: fearful cues=2.12, neutral cues=5.24; $F(1, 30)=225.539$, $P<0.001$) but were matched in arousal (mean: fearful cues=6.10, neutral cues=5.92; $F(1, 30)=1.235$, $P=0.275$).

1.3 Procedure

Cueing status (cued or uncued) and emotion (fearful or neutral) were the two manipulated variables in this experiment.

Therefore, there were four conditions in the experiment: neutral cued-neutral, fearful cued-fearful, uncued-neutral, and uncued-fearful faces. The experiment consisted of four blocks, with each block including 64 trials equally distributed into four conditions. In other words, each block contained 16 trials for each condition. The onset sequence of the four conditions was randomized across trials. Prior to the experiment, 20 practice trials were used to familiarize participants with the experimental procedure. Participants were seated in a quiet room at approximately 150 cm from a computer screen, with the horizontal and vertical visual angles below 6° . Prior to the experiment, participants were instructed to determine the gender of the faces that were presented. They were told that the faces would sometimes be preceded by contextual images that were semantically related to facial expressions. Each trial was initiated by a 500 ms presentation of a small black fixation cross on the white computer screen. A white blank screen of a random duration between 500 and 1000 ms was followed by the presentation of either a cue image or the fixation cross (i.e., no cue) for 500 ms. Participants were instructed to passively view the cue pictures or the cross. The cue image or cross was then replaced by a variable 500–1000 ms blank screen, which was then followed by a face stimulus for 500 ms. The gender of the face stimuli was balanced in both the cued and uncued conditions. Half of the participants were instructed to press the “F” key on the keyboard as accurately and quickly as possible with their left index finger for male faces, and to press the “J” key with their right index finger for female faces. These responses were reversed for the other half of the participants. After the EEG recording, a post-experiment debriefing session was conducted, in which participants reported their feelings about stimulus features and their performance in the task.

1.4 ERP recording and analysis

EEG was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Products), with an average reference on the left and right mastoids and a ground electrode on the medial frontal aspect. The vertical electrooculogram (EOG) was recorded supra- and infra-orbitally at the left eye. The horizontal EOG was recorded from the left versus right orbital rim. The EEG and EOG were amplified using a DC-100 Hz bandpass, and continuously sampled at 500 Hz/channel. Each inter-electrode impedance was maintained below 5 k Ω . Averaging of ERPs was performed off-line. Trials containing EOG artifacts (mean EOG voltage exceeding $\pm 80 \mu\text{V}$) and those contaminated with artifacts due to amplifier clipping or peak-to-peak deflection exceeding $\pm 80 \mu\text{V}$ were excluded from averaging.

The EEG activity associated with correct responses in each condition was averaged separately. Thus, four types of ERPs, composed of each combination of cueing status (cued vs. uncued) and emotion (fearful vs. neutral), were obtained

(i.e., neutral cue and neutral faces, fearful cue and fearful faces, no cue and neutral faces, no cue and fearful faces). To test whether cue-induced emotional effects (i.e., participants expected the emotions of subsequent faces) were significant, the ERP waveforms were first time-locked to the onset of cue pictures. The average epoch was 800 ms, including a 200 ms pre-stimulus baseline (Figure 1). An enhanced negativity was induced by fearful relative to neutral cues across frontal sites, which began at about 200 ms and ended at about 600 ms post stimulus. Thus, the following nine centro-frontal sites: Fp1, Fp2, Af3, Af4, Fz, FC3, FC4, FCz and Cz, were selected to analyze cue-induced emotional effects. A repeated measures analysis of variance (ANOVA) was conducted on the averaged amplitudes during 250–350 ms, 350–450 ms, and 450–550 ms intervals, with emotion (fearful or neutral) and nine electrode sites as repeated factors.

Subsequently, the ERP waveforms were time-locked to the onset of face stimuli. The average epoch was 1200 ms, including a 200 ms pre-stimulus baseline. As shown in Figure 2, face images, irrespective of emotion and cueing status, induced a prominent face-sensitive P2 (vertex positive potential, VPP) component. Additionally, all facial expressions elicited an early N1 (80–130 ms) component and later N200 (200–350 ms) activity. Thus, the following 12 electrode sites were selected for statistical analysis: Fz, FCz, FC3, FC4, Cz, C1, C2, C3, C4, CP1, CP2 and Pz. The amplitudes (baseline to peak) and peak latencies of the N1 (80–110 ms) and the P2 (130–180 ms) components were measured and analyzed with cueing status (cued or uncued), emotion (fearful or neutral) and 12 electrode sites as factors. In addition, the averaged amplitudes for facial expressions during the 200–350 ms interval, in which pronounced differences across the four conditions were displayed, were measured accordingly. A repeated measures ANOVA was conducted for the averaged amplitudes at 200–250 ms, 250–300 ms, and 300–350 ms intervals, respectively. The degrees of freedom of the *F*-ratio were corrected using the Greenhouse-Geisser method.

2 Results

2.1 Behavioral data

Only trials with correct responses and a reaction time (*RT*) under 1000 ms were included in the analyses. Mean *RT*s and accuracy are shown in Table 1. The two-way repeated measures ANOVA of *RT* with cueing status (cued or uncued) and emotion (fearful or neutral) as factors did not demonstrate a significant main effect of cueing status ($F(1, 13)=1.22, P=0.29$) or emotion ($F(1, 13)=0.98, P=0.34$), or a significant interaction between cueing status and emotion ($F(1, 13)=0.14, P=0.72$). However, an analysis of accuracy revealed a significant interaction between cueing status and

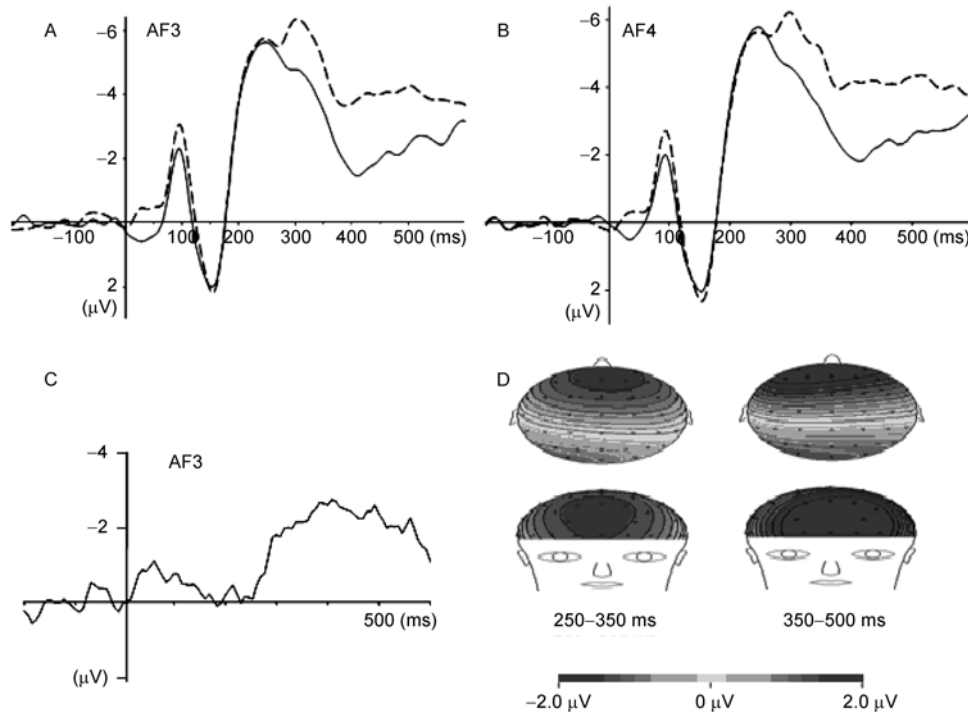


Figure 1 A and B, Averaged ERPs elicited by fearful (dashed lines) and neutral (solid lines) cue pictures at AF3 and AF4. C, Fearful-neutral difference ERPs at AF3. D, Topographical distribution of the difference ERPs at 250–350 ms and 350–500 ms post pictures.

emotion ($F(1, 13)=6.12, P<0.05$). Further analysis of this interaction effect demonstrated that the accuracy rate of gender discrimination was not significantly different between fearful and neutral faces in the cued condition ($P>0.1$), but was significantly lower for fearful than for neutral faces in the uncued condition ($P<0.01$). This suggests that the salient emotional content of unexpected fearful faces may have distracted participants' attention from the task. However, the distracting effect that arose from negative bias [5–7] was attenuated when the appearance of fearful faces was predictable.

2.2 ERP data

2.2.1 Effect of cue emotion

As shown in Figure 1, fearful cues elicited larger negative deflections than neutral cues over frontal-central recording sites during the 250–600 ms interval. A two-way repeated measures ANOVA conducted on the averaged amplitudes revealed a significant effect of emotion during the 250–350 ms ($F(1, 13)=5.73, P<0.05$), 350–450 ms ($F(1, 13)=12.03, P<0.01$), and 450–550 ms ($F(1, 13)=4.70, P<0.05$) intervals. However, the effect of emotion on amplitude was not significant in the 550–600 ms interval ($F(1, 13)=3.31, P>0.05$). Thus, fearful cues elicited a clear effect of emotion during the 250–550 ms interval. Participants were thus able to predict the presentation of fearful expressions from the detection of fearful cues. Consistent with these observations, par-

ticipants reported in the interview session that some of the cue pictures were fearful and emotionally unpleasant, and that these pictures consistently preceded the presentation of fearful faces.

2.2.2 Effect of expectation on the neural sensitivity to fearful faces

The analyses of N1 amplitudes showed no significant main or interaction effects. The analysis of N1 latencies did not reveal any cue and emotion interaction effect, but did reveal a significant main effect of cue ($F(1, 13)=9.89, P<0.05$) and emotion ($F(1, 13)=8.48, P<0.05$). Cued faces (95 ± 2.01 ms) elicited longer N1 latencies than non-cued faces (91 ± 1.82 ms) and peak latencies were shorter for fearful (92 ± 1.87 ms) than for neutral (94 ± 1.91 ms) faces. Thus, neither the N1 amplitude or latencies revealed a significant interaction between emotion and cue, suggesting that the effect of expectation on neural sensitivity to fearful faces may occur at a later point in processing.

The ANOVA examining P2 amplitude revealed a significant main effect of cueing status ($F(1, 13)=27.63, P<0.001$). P2 amplitude was larger for uncued (16.02 ± 1.23 μV) than for cued (12.69 ± 1.17 μV) faces, irrespective of face emotion. Moreover, the main effect of emotion and the interaction between emotion and cueing status were both significant ($F(1, 13)=5.34, P<0.05$; $F(1, 13)=5.40, P<0.05$). The further analysis of the emotion and cueing status interaction effect revealed increased amplitudes for fearful

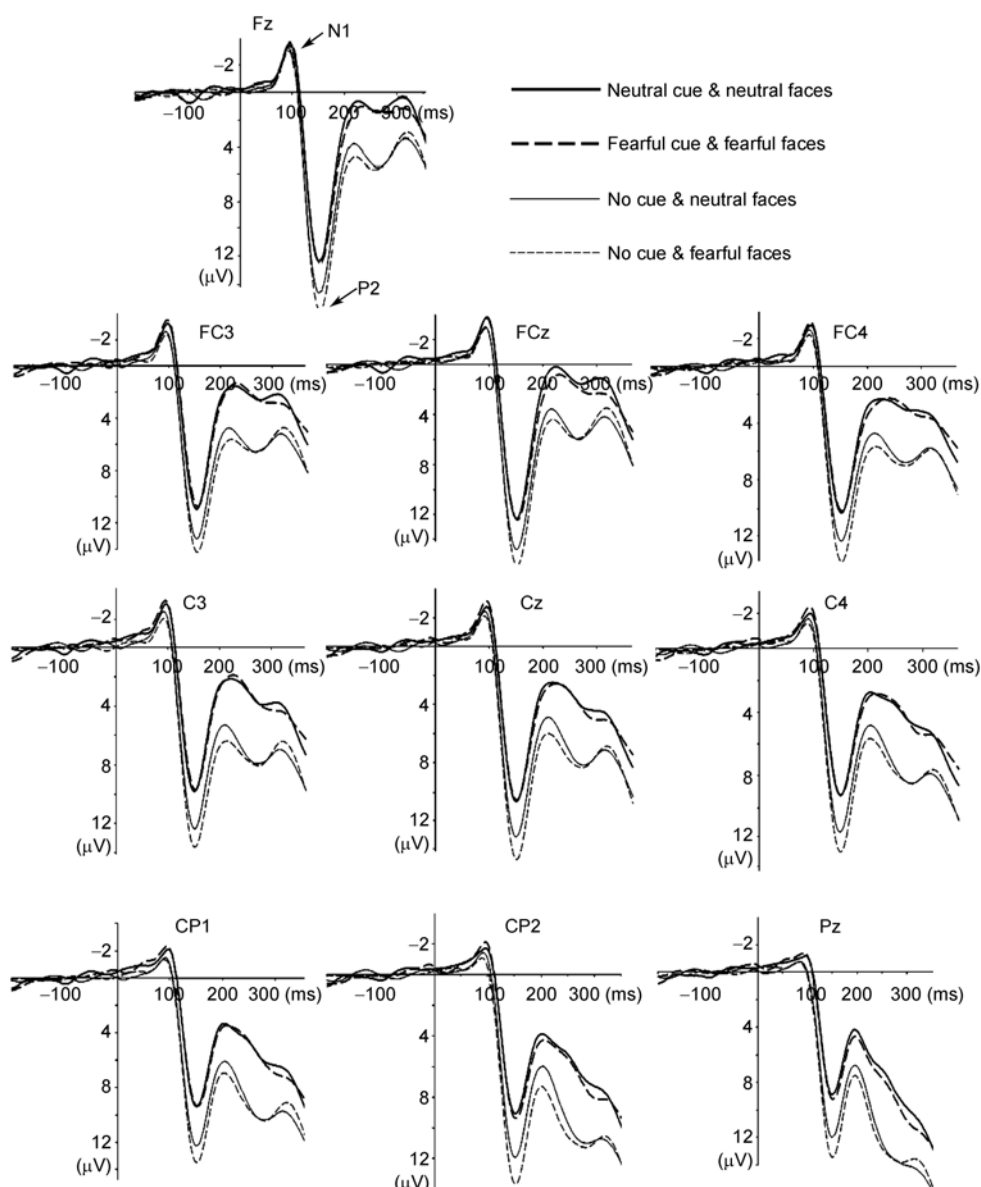


Figure 2 Averaged ERPs elicited by cue-free neutral (thin solid lines) and fearful (thin dashed lines) faces, and by cued neutral (bold solid lines) and fearful (bold dashed lines) faces at frontal (Fz), frontocentral (FC3, FCz and FC4), central (C3, Cz and C4) and posterior-parietal (CP1, CP2, and Pz) sites.

Table 1 Mean reaction times and accuracy rates for fearful and neutral facial expressions under cue and no cue conditions (mean±SE)

	Reaction time (ms)		Accuracy rate (%)	
	Fearful	Neutral	Fearful	Neutral
Cue condition ('expected')	568±16	563±14	94±1.4	94±1.3
No cue condition ('unexpected')	577±17	572±18	92±1.7	96±1.2

((16.79±1.31) μV) compared with neutral faces ((15.24±1.19) μV) during the uncued condition ($F=13.23, P<0.01$). By contrast, the amplitude differences between fearful ((12.86±1.29) μV) and neutral faces ((12.51±1.10) μV) were not significant in the cued condition ($F=0.41, P>0.05$). The analysis of P2 latency revealed no significant main or

interaction effects.

The averaged amplitudes for the 200–350 ms interval were separately analyzed in 200–250, 250–300 and 300–350 ms intervals. The repeated measures ANOVA in these intervals revealed a significant main effect of cueing status at each of the three intervals ($F(1, 13)=14.98, P<0.05$; $F(1, 13)=9.35, P<0.01$; $F(1, 13)=5.54, P<0.05$). Moreover, the interaction effect between cueing status and emotion was only significant at the 200–250 ms interval ($F(1, 13)=6.04, P<0.05$). Further analyses of the interaction effect revealed significant differences between fearful ((7.99±1.09) μV) and neutral ((7.00±0.96) μV) facial expressions during the uncued condition ($F=6.28, P<0.05$). Conversely, the amplitude differences between fearful ((4.48±0.56) μV) and neutral

((5.10 ± 0.65) μV) faces were not significant under the cued condition ($F=2.363$, $P>0.05$). Therefore, the present study revealed clear emotional responses to unexpected fearful faces. However, emotional reactions were attenuated when the appearance of fearful faces was expected (Figure 3).

3 Discussion

The present study used ERP measures to investigate the influence of expectation on neural sensitivity to fearful facial expressions. Images with an emotional valence that predicted the emotional expressions of subsequently presented faces were used as cues. An uncued condition was used as a baseline, so that the effect of expectation could be analyzed. In accord with our hypothesis, we observed an effect of expectation on neural sensitivity to fearful facial expressions. The behavioral data revealed a significant interference effect of fearful emotional expression in the uncued condition, such that performance in a gender discrimination task was significantly lower for unpredictable fearful expressions compared with unpredictable neutral expressions. In accord with the notion that negative bias leads to the preferential processing of unpleasant emotional stimuli [21–24], our results suggest that the emotional salience of unexpected fearful faces engaged participants' attention automatically, resulting in a reduction in the amount of central processing resources available for task-relevant processing and ultimately impairing performance in the gender discrimination task. By contrast, no such interference effect was apparent when the presentation of fearful facial expressions was predictable. A similar accuracy rate of gender discrimination was observed for both fearful and neutral

faces during the cued condition. These behavioral observations were supported by the ERP data, which revealed similar neural activity in response to fearful and neutral facial expressions in the cued condition (Figure 2). By contrast, stronger neural responses were observed in response to unexpected fearful faces within the P2 and 200–250 ms intervals in the uncued condition.

In the present study, fearful cues elicited increased negative deflections compared with neutral cues during an interval 250–550 ms after the onset of the cue image. This suggests that fearful cues, consistent with the fear ratings we obtained (see Materials and methods), induced pronounced emotional reactions relative to neutral cue pictures. Because fearful cue pictures were always followed by the onset of fearful faces and neutral cues were always followed by neutral faces, participants could learn that fearful faces would be presented immediately following presentation of a fearful cue picture. In fact, participants reported after the experiment that the onset of neutral cue pictures indicated the follow-up presentation of neutral facial expressions, and fearful cue pictures consistently preceded the presentation of fearful faces. Therefore, the onset of fearful faces and that of neutral faces were both predictable in the cued condition because the valence of cues indicated the emotional expression of the subsequent faces.

When participants expected the expression of the face stimulus (in the cued condition), they did not react more intensely to fearful faces than to neutral faces at P2 and 200–250 ms intervals. Previous ERP studies have consistently reported a face-sensitive VPP at 120–220 ms post stimulus, with the largest amplitude at central sites when mastoid or earlobe references were used [42–44]. Thus, the P2 elicited by faces in the current study, for which the larg-

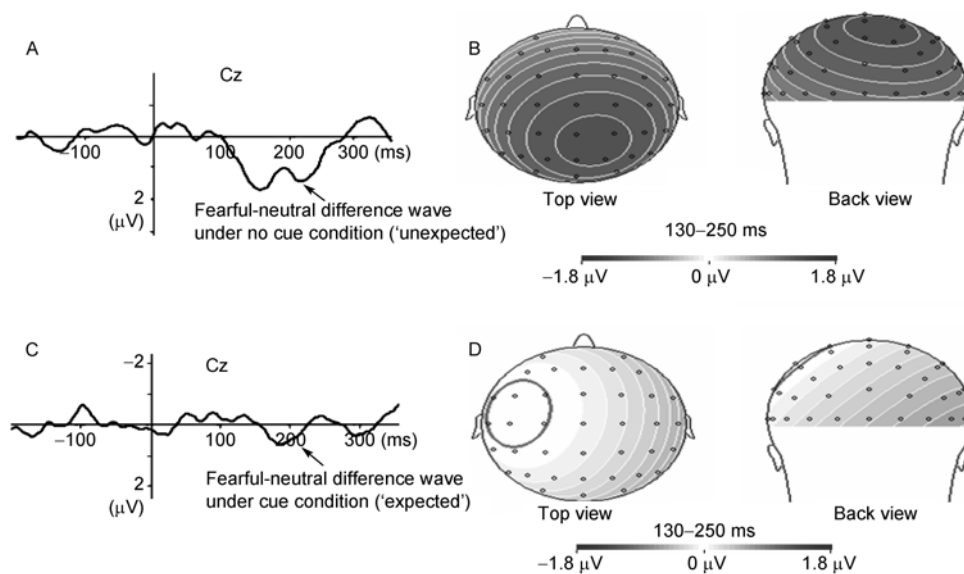


Figure 3 Fearful face/neutral face difference ERPs at Cz (A and C) and their topographical maps (B and D). A and B, difference ERPs and their topographical maps under the uncued ('unexpected') condition. C and D, difference ERPs and their topographical maps under the cued ('expected') condition.

est amplitude was recorded over the central areas (Figure 2), had a peak latency and morphology similar to the classic VPP component archetype. A number of studies have demonstrated larger amplitudes for fearful compared with neutral faces in the VPP and later components [3,7,30,46,47]. Therefore, the absence of an effect of emotion on VPP amplitudes in the cued condition is distinct from, but not inconsistent with, the previous observations of numerous facial emotion studies where fearful facial expressions were presented in an unpredictable manner [30,45,46].

In real-life settings, prior awareness of upcoming salient events can facilitate an individual's mobilization of cognitive resources and behavioral measures. As a result of preparation, the individual may cope better with potential danger. Accordingly, the strength of their emotional reactions is reduced when they are in a prepared state [15]. Thus, it may not be surprising that we found similar neural responses to fearful and neutral faces during the cued condition. On the other hand, consistent with previous observations [30,45,46] we found that neural responses to unpredictable fearful faces were more pronounced than responses to unpredictable neutral faces. This finding may be related to the evolutionary importance of devoting attention to unexpected salient events [4].

Our behavioral and ERP data both revealed an effect of expectation on human sensitivity to fearful facial expressions, with emotional responses to fearful faces more pronounced in unpredictable compared with predictable conditions. These findings were supported by evidence from expectation-related studies of outcome evaluation [12,13,16,47]. For instance, a recent study addressing the interaction between expectation and feedback processing reported larger amplitudes of feedback-related negativity (FRN)—a negative ERP deflection elicited by monetary loss—when the negative outcome was unpredictable compared with when the feedback was predictable [12,13]. Moreover, FRN amplitude was found to vary depending on the valence of the unpredictable outcome, whereas this effect was smaller when feedback was predictable [12].

In addition, the present study revealed significant main effects of cueing status and emotion on N1 latencies. Peak latencies of N1 were shorter for fearful versus neutral faces, irrespective of cueing status. This suggests that fearful faces, because of their biological importance, elicited faster visual attentional processing compared with neutral faces [3,7]. Moreover, N1 latencies were longer for cued than for uncued faces (Figure 2). On the other hand, the detection of cue valence, and the subsequent expectation and confirming emotions of facial expressions were all task-irrelevant processes that may have interfered with gender identity processing in the cued condition. Conversely, the central processing of gender was less affected, and participants allocated more resources for task performance during the uncued condition. This may explain the longer latencies of N1 in the cued versus uncued conditions, irrespective of

facial emotion. In line with this interpretation, neural responses to facial expressions were larger during the uncued condition across P2 and 200–350 ms intervals (Figure 2), in the absence of cognitive control over task-irrelevant processes, in accord with previous reports [3,48,49].

4 Conclusion

The present study revealed that human sensitivity to fearful faces depended on emotional expectation. Thus, although humans are sensitive to unpredictable fearful stimuli, sensitivity to fearful stimuli can be decreased by emotional expectation.

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